

BLOOD CIRCULATION IN FOUR SPECIES OF BARNACLES (*LEPAS*, *CONCHODERMA*: LEPADIDAE)

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ABSTRACT.—Circulatory morphologies of the primitive lepadomorphans *Lepas anatifera*, *L. pectinata pacifica*, *L. fascicularis* and *Conchoderma virgatum* are similar, but major differences appear in vessel caliber and refinement of the basic system. The smaller species (*L. fascicularis* and *L. pectinata pacifica*) have larger vessels for their body size than the larger species (*L. anatifera* and *C. virgatum*). Circulatory organization of the lepadids is simpler than that of *Pollicipes polymerus* (Scalpellidae) and *Balanus tintinnabulum* (Balanidae). The lepadid rostral vessel, which is morphologically similar to that of *P. polymerus*, is interpreted as a vestige of the heart. Pump function can be attributed to the rostral sinus (the blood pump), which is apparently a remnant of the pericardial sinus. Transfer of hemolymph pumping from the heart to the rostral sinus probably occurred with the development of the peduncle.

Detailed accounts of cirriped circulation may be found in Cannon (1947) and Burnett (1972). The circulatory systems of *Lithotrya valentiana* and *Pollicipes polymerus* (Cannon, 1947) had been considered to represent the general condition for thoracican Cirripedia (e.g. Maynard, 1960). However, Burnett (1972) showed that the circulatory system of the pedunculate barnacle *Pollicipes polymerus* was unlike that of other Crustacea. In order to obtain a more complete understanding of circulatory relationships in the Cirripedia, I studied the circulatory systems of four species of Lepadidae: *Lepas anatifera*, *L. pectinata pacifica*, *L. fascicularis* and *Conchoderma virgatum*.

MATERIALS AND METHODS

The three species of *Lepas* were collected from debris that washed ashore at Scripps Institution of Oceanography, La Jolla, California in the summers of 1972 and 1973. The *Conchoderma virgatum* were collected from a Pacific Ridley sea turtle (*Lepidochelys olivacea*) captured off La Jolla. Living specimens were injected with yellow (MV-122) or maroon (MV-118) Microfil (Canton Bio-Medical Products, Inc. P.O. Box 2017, Boulder, Colorado 80302), either into the peduncle or through the adductor scutum into the rostral sinus, following techniques developed in an earlier study (Burnett, 1972). The amount injected ranged from 0.5 to 2.0 ml based on the size of the animal. In each species, the rostral valve at the posterior-most part of the peduncular vessel usually did not hold under the pressure exerted from the Microfil injections into the peduncle; almost always a significant amount of Microfil entered the body via the peduncular vessel. The rostral valve in the lepadids is more delicate than that of *P. polymerus*; consequently their vessels are more prone to rupture and distort, which makes it difficult to trace circulatory pathways, especially with the peripheral-collecting circulation. In order to determine vessel wall structure, portions of the gut vessels were removed (while they still had solidified Microfil in the vessel lumina) and embedded in Spurr (Polysciences, Inc. Paul Valley Industrial Park, Warrington, Penna. 18976). Sections, 2 μ m thick, were made with a glass knife on a Porter-Blum JB-4 microtome.

Body movements of *L. fascicularis* were observed through a dissection microscope by shining a light through the thin walled capitulum.

CIRCULATORY MORPHOLOGY

Basically, I shall follow Burnett (1972) in dividing the barnacle circulatory system into three arbitrary divisions: 1) the circulation of the peduncle and mantle, 2) the distributive circulation and 3) the peripheral-collecting circulation.

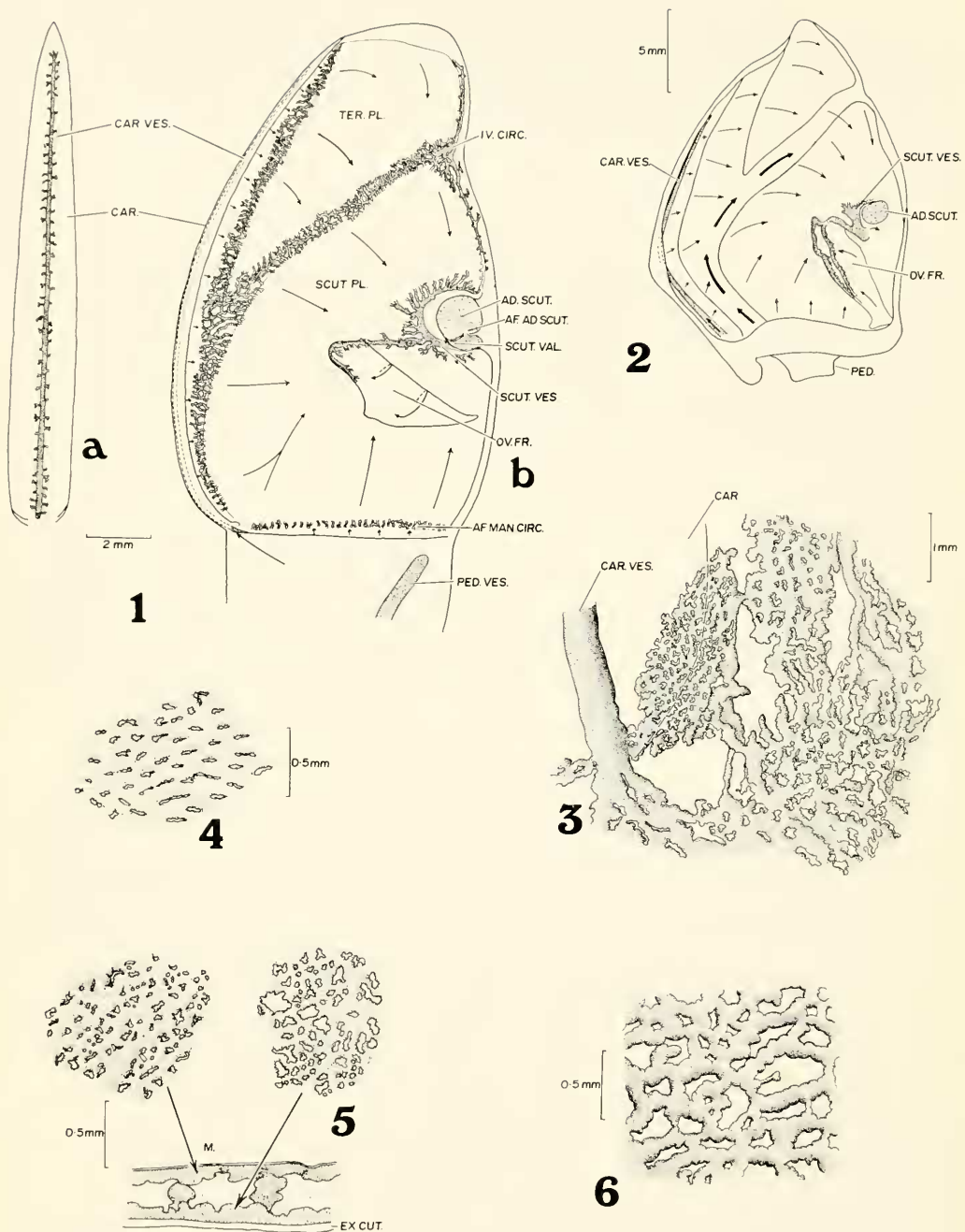


Figure 1. Mantle circulation in *L. anatifera*. a. View of the carina with the carinal vessel situated along the midline of the valve. b. View of the right side of the mantle and a portion of the peduncle. Only the intervalve circulation is shown, with the arrows representing the direction of hemolymph flow. Basically, this pattern of circulation is present in *L. pectinata pacifica* and *C. virgatum*. Abbreviations are explained in the Appendix.

Figure 2. Mantle circulation (right side) in *L. fascicularis*. Arrows show the direction of flow with the heavier arrows indicating major hemolymph flow.

Figure 3. The origin and associated circulation of the carinal vessel in *L. fascicularis*.

Figure 4. A portion of the tergal plexus from *L. pectinata pacifica*.

Figure 5. The double circulation of the mantle in *C. virgatum*.

Figure 6. A portion of the tergal plexus from *L. anatifera*.

Circulation of the peduncle and mantle.—The peduncular vessel extends the full length of the peduncle without giving off any branches, and ends with a gradual enlargement at the basal disc. From the basal disc, the hemolymph percolates towards the mantle, and it appears that the entire peduncle is a single sinus.

Hemolymph from the peduncle enters the mantle circulation by two pathways (Fig. 1). In one route, blood is directed into the mantle circulation from the posterior-most part of the peduncle by a series of short parallel vessels (Fig. 1b). From these vessels the blood moves through a plexus toward the ovigerous frena and eventually into the paired scutal vessels. *Lepas fascicularis* has enlarged vessels entering the mantle in the area between the scutal and carinal regions (Figs. 2, 3).

The other pathway by which the blood enters the mantle is through the carinal vessel (Figs. 1-3). In *Lithotrya valentiana*, Cannon (1947) described a pair of vessels in the mantle region between the terga and carina, but I doubt these are homologous to the carinal vessel of the Lepadidae, which is unpaired. The carinal vessel extends the full length of the carina, and gives off smaller vessels along its entire length. Almost all of the tergal area and a good portion of the scutal area of the mantle is supplied by this vessel.

In lepadids, the ovigerous frena (Figs. 1, 2) are highly vascularized with a circulation similar to the rest of the mantle. A vessel, connecting the scutal vessel on each side of the mantle, borders the distal margin of each ovigerous frenum. In *L. fascicularis*, the ovigerous frena are bilobate (Fig. 2), with a large vessel extending along the distal margin of each lobe. These vessels join and the resulting vessel connects to the scutal vessels, which in turn enter the body. In contrast to the situation in *P. polymerus*, the mantle knobs and the circulation associated with the mantle muscles are not present in the lepadids.

The paired scutal vessels partially circle the adductor scutorum at the muscle's insertion on the two scutal plates (Figs. 1, 2) in a manner similar to that found in *P. polymerus*. The scutal valve (Fig. 1) lies just inside the entrance of the scutal vessel into the body.

The circulation of the mantle varies between species (Figs. 3-6), with the plexuses appearing random in *L. anatifera* (Fig. 6) to fairly organized in *L. pectinata pacifica* (Fig. 4). The mantle circulation of *C. virgatum* (Fig. 5) differs from *Lepas* in being essentially a double system in which plexuses are associated with both the external and internal cuticles of the capitulum. Scattered connections exist between these two plexuses.

In *L. anatifera*, the vessels between the capitular plates enlarge somewhat; in *C. virgatum* the plexal vessels appear uniform throughout the mantle, but enlarge as they approach the scutal vessels.

Distributive circulation.—Near the points where the adductor scutorum inserts on the scuta, the two scutal vessels enter the body from the mantle and enlarge to form the paired scutal sinuses (Figs. 7-10). In all four species, as in *P. polymerus*, the scutal sinuses are located on each side of the rostral sinus, in close proximity to the adductor scutorum. The precise position of the scutal sinuses varies from species to species: in *L. anatifera* they are mostly posterior to the adductor scutorum; in *L. fascicularis* they are anterior; and in *L. pectinata pacifica* and *C. virgatum* they are dorsal. Their shape and extent also varies.

The adductor scutorum receives blood from the scutal sinuses in all species. The afferent circulation to this muscle is located immediately posterior to the scutal valves. From the scutal sinuses hemolymph enters the vessels of the gut, gastric gland, and the maxillary gland.

On the gut, the gastric plexus continues around most of the cephalic portion of the gut with little variation in vessel caliber (Figs. 7-10). In the posterior part of the cephalic gut, the paired inferior gastric vessels continue from vessels of the gastric plexus. As this pair of vessels continues posteriorly, branches of the gastric gland plexus also combine with the inferior gastric vessels.

The paired inferior gastric vessels join on the ventral surface of the thoracic gut above the first pair of cirri. This combined vessel (the posterior inferior gastric vessel) continues posteriorly and descends to contact the epineural sinus by one or more

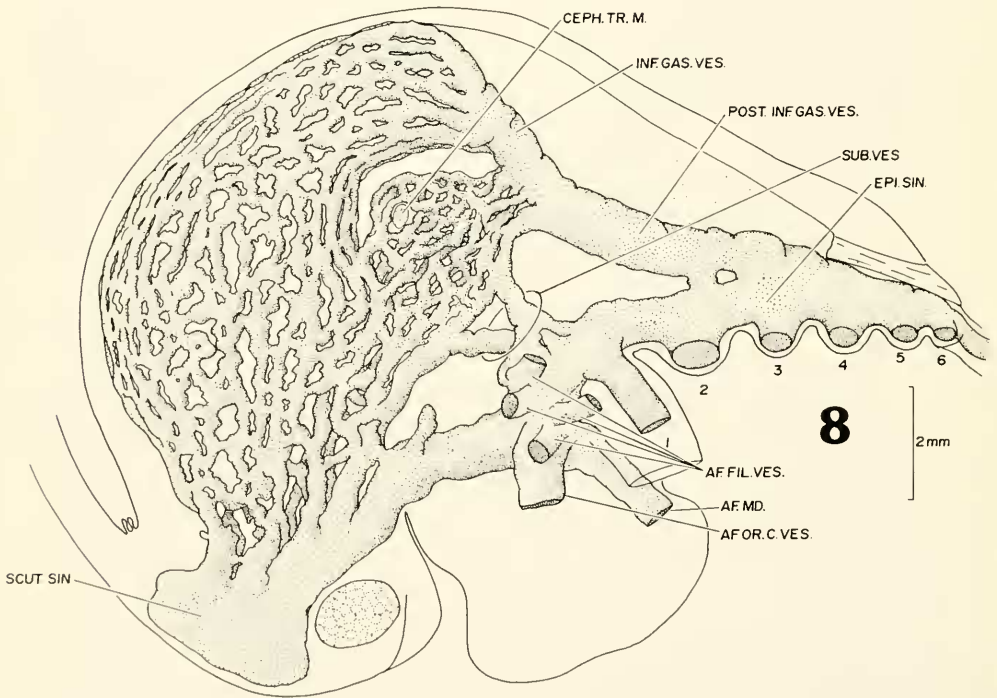
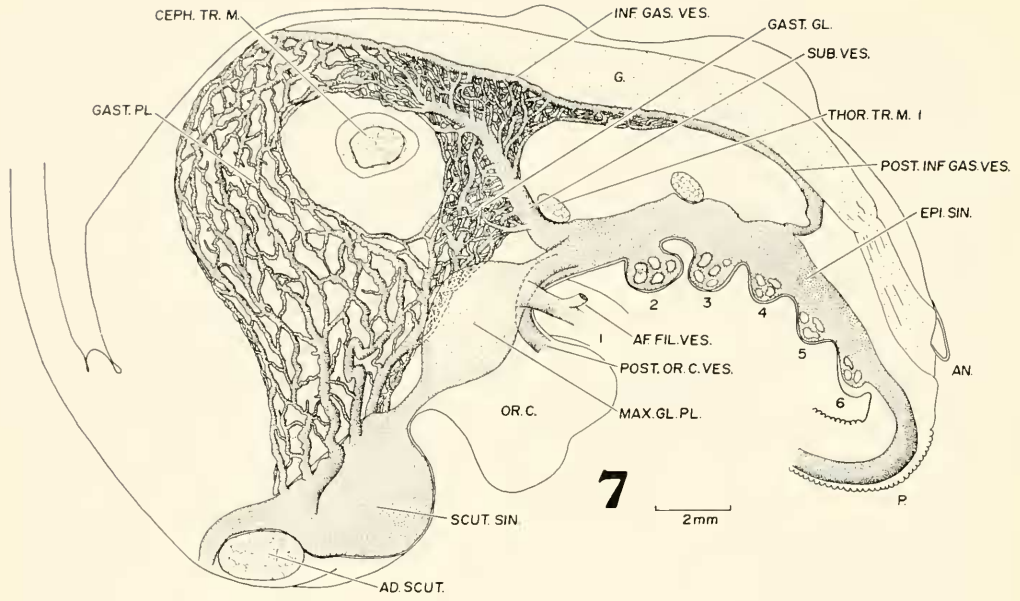


Figure 7. Distributive circulation as seen from the left side of the body in *L. anatifera*. Numbers 1-6 refer to the positions of the respective cirri.

Figure 8. Distributive circulation in *L. fascicularis*.

branches. In *L. anatifera*, the posterior inferior gastric vessel is reduced and has only one contact with the epineural sinus. In all lepadids, the epineural sinus, which surrounds the nerve cord at the base of the cirri, receives blood from two additional sources: 1) the scutal sinuses through the maxillary gland, to connect to the anterior part of the epineural sinus, and 2) a connection by the subintestinal vessel from the gastric gland

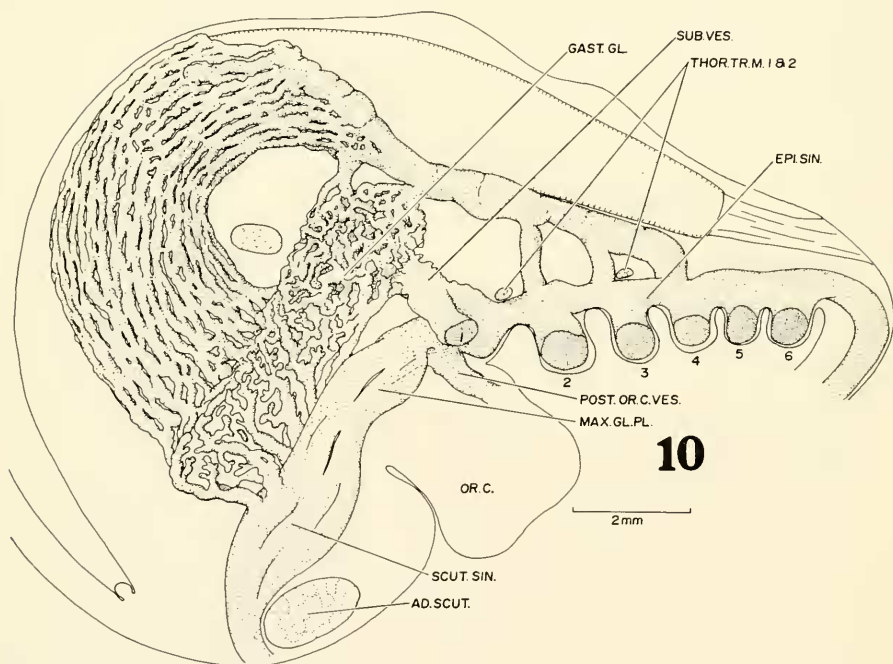
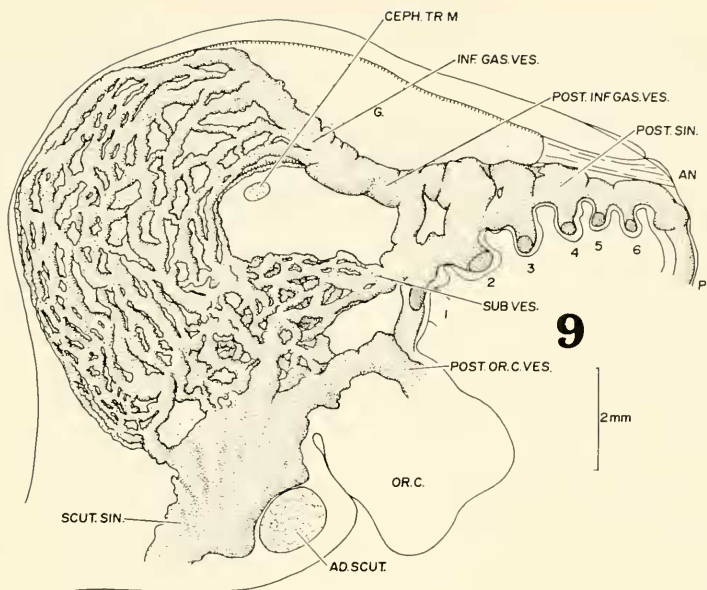


Figure 9. Distributive circulation in *L. pectinata pacifica*.

Figure 10. Distributive circulation in *C. virgatum*.

plexus. Blood from the epineurial sinus goes to the cirri, penis and oral cone.

In *L. anatifera* the subintestinal vessel originates as a pair of vessels among the plexus surrounding the gastric gland. These two vessels collect blood from the gastric gland plexus and enlarge as they descend toward the epineurial sinus. The subintestinal vessel is then formed by the combining of the two vessels just anterior to the first thoracic transverse muscle. On the anterior part of the epineurial sinus, the subintestinal vessel

enters slightly dorsal to the maxillary gland connections. In the other three species the subintestinal vessel consists of one or two short vessels connecting the gastric gland plexus to the epineural sinus.

The distributive circulation of *L. fascicularis* is more grossly constructed in contrast to *L. anatifera*. The posterior inferior gastric vessel unites with the epineural sinus to form a large posterior sinus. The afferents to the oral cone, which originate from the epineural sinus, are divided into two vessels, the afferent mandibular vessel going directly to the mandibles, and the afferent oral cone vessel to the rest of the oral cone. The afferent filamentary vessels to the four filamentary appendages at the base of each first cirrus originate on the anterior-most part of the epineural sinus.

Circulatory morphology in *L. pectinata pacifica* appears most similar to that of *L. fascicularis*. The union of the posterior inferior gastric vessel to the epineural sinus is so extensive that the two make up a single sinus (the posterior sinus) posterior to the second thoracic segment. The gastric gland plexus does not extend directly around the cephalic transverse muscle and the large sinus at the base of the first cirrus is not present as it is in *L. fascicularis*.

The distributive system of *C. virgatum* is similar to that of *Lepas* (Fig. 10). The gut plexus is strongly directionally oriented. The connection of the posterior inferior gastric vessel to the epineural sinus is by two or three large caliber vessels. Plexal circulation of the gastric gland appears more haphazard than in *L. anatifera*. The dorsal part of the gastric circulation is connected to the inferior gastric vessels by a varying number of short vessels.

In *P. polymerus*, the cirri are too darkly pigmented to observe their circulatory morphology, but the opposite holds with the lepadids. Figure 11 shows the circulation of three segments of a ramus from *L. anatifera*, which is similar to that of the other species being considered here.

The afferent circulation in a ramus of a cirrus continues distally from the epineural sinus and is in close contact with the flexor muscle. In each segment of a ramus, the circumflexor muscle circulation originates from the afferent vessel and surrounds the flexor muscle in a sheet-like sinus. This circulation connects to the efferent circulation of the ramus by a steadily constricting sinus. There may be a valve at the contact point with the efferent cirral vessel. The efferent cirral vessel progresses down the outside margin of the ramus to eventually connect with the peripheral-collecting circulation.

The general morphology of circulation in the lepadid filamentary appendage is similar to that of *P. polymerus* (Burnett, 1972). There are two vessels (the filamentary vessels) on opposite sides of the filamentary appendage that parallel the main axis of the appendage (Fig. 12). From the afferent filamentary vessel, a sheet-like sinus arises on each side of the vessel, and each extends in a semicircle around the filamentary appendage to connect the efferent filamentary vessel.

The Lepadidae have two types of filamentary appendages: type I receives hemolymph from the afferent circulation to the cirri; type II receives blood from the peripheral circulation and will be discussed below. Each species shows a different arrangement and number of type I filamentary appendages. *Lepas anatifera* has a type I appendage at the base of the first cirrus. *Lepas pectinata pacifica* also has one in the same location, but it is reduced. There are four such appendages in *L. fascicularis*, which form a star pattern where they originate at the base of first cirrus. *Conchoderma virgatum* has filamentary appendages of the first type at the base of the first, third, fourth and fifth cirri. Interestingly, *C. virgatum* has an additional filamentary appendage at the base of the first cirrus that receives blood from the efferent circulation of that cirrus (a type II filamentary appendage). This is the only case where a type II filamentary appendage occurs on a cirral base.

Peripheral-collecting circulation. (Figs. 13-18).—In *P. polymerus*, I described three circulations of the body: distributive, peripheral and collecting. The lepadids, however, have only two distinctive circulations of the body, the distributive and the return. In order to maintain uniformity in nomenclature, I shall call the return circulation of the lepadids the peripheral-collecting circulation. Cannon (1947) also described the return circulation

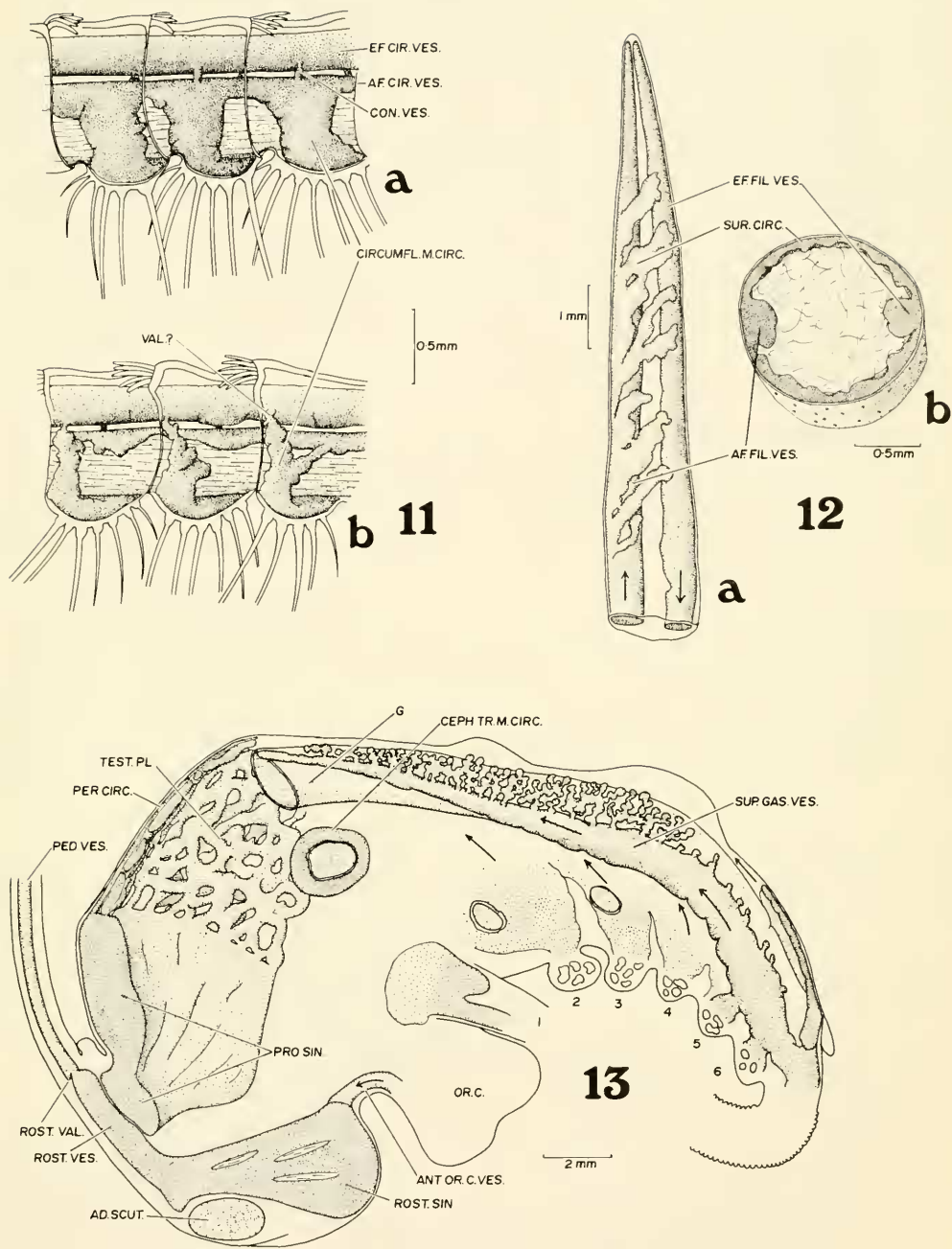


Figure 11. Circulation of three segments of a ramus in *L. anatifera*. a. View of the posteriorly facing side of the ramus, b. anteriorly facing side.

Figure 12. A filamentary appendage from the base of the first cirrus in *L. anatifera* showing the circulatory pattern. This arrangement is basic to all filamentary appendages thus far observed. a. Longitudinal view, b. cross section.

Figure 13. The peripheral-collecting circulation of *L. anatifera* in an illustration similar to Fig. 7. The superior gastric vessel along most of its length abutts directly against the inferior gastric vessel (see Fig. 7).

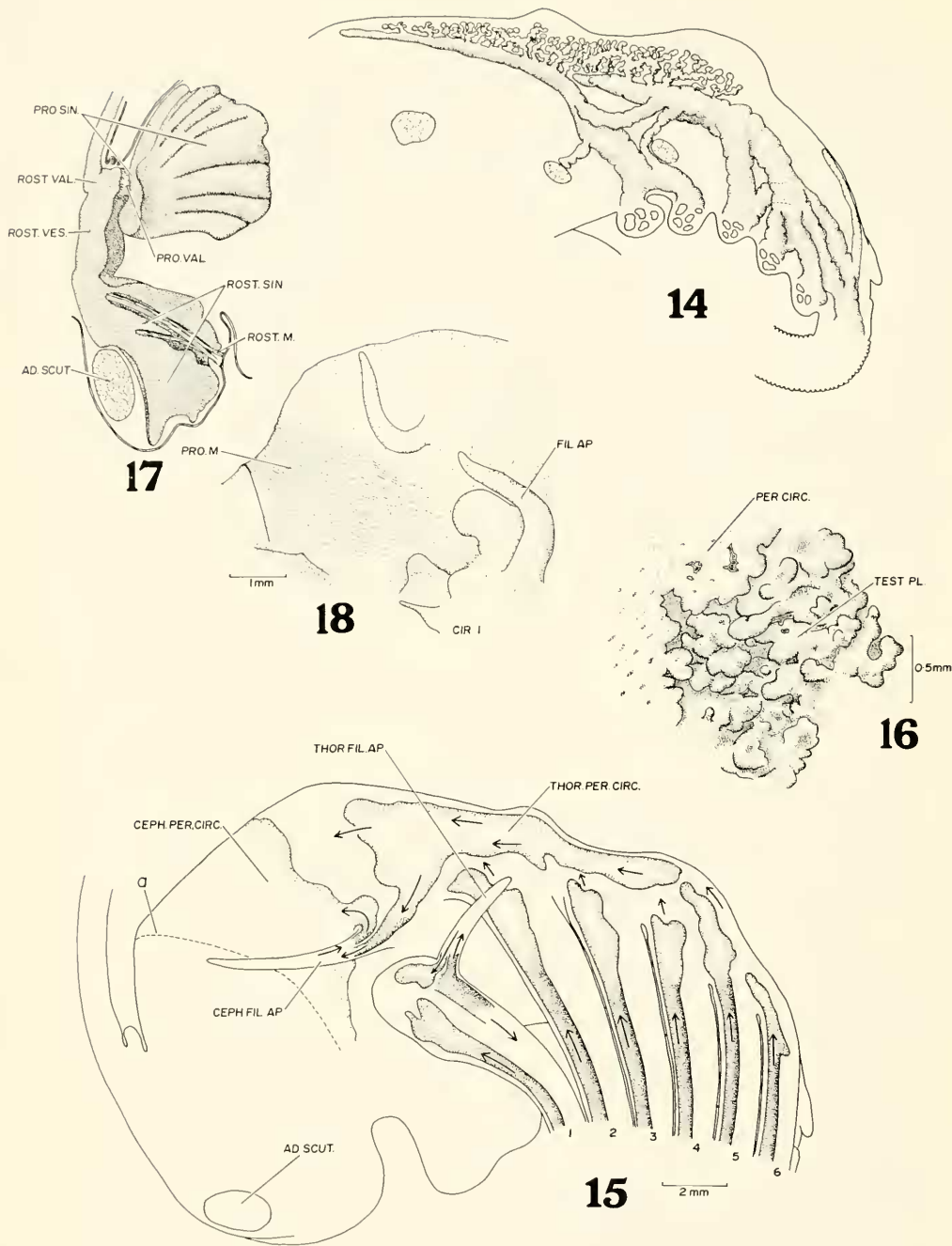


Figure 14. Variation in the superior gastric vessel of *L. anatifera*. See text for description.

Figure 15. The peripheral-collecting circulation as seen from the left side of the body of *L. anatifera*, a, the border of the prosomal sinus.

Figure 16. Close-up of the peripheral-collecting circulation of the cephalic region in *L. fascicularis* showing the thin layer of the peripheral circulation along with the testicular plexus.

Figure 17. The rostral vessel and its associated sinuses in *L. anatifera*.

Figure 18. The distribution of the thin layer of muscle surrounding the prosomal sinus in *C. virgatum*.

in *Lithotrya valentiana* as essentially a peripheral-collecting system.

The peripheral-collecting circulation in the Lepadidae was much more difficult to trace due to the weakness of the rostral valve and a consequent filling of the prosoma with Microfil. However, in a few *L. anatifera* I was able to trace this circulation, although fine details were usually obscured.

The major source of hemolymph to the peripheral-collecting circulation comes from the efferent cirral vessels and the return flow from the penis. There are two possible routes for this hemolymph after it leaves the cirri. In one pathway, vessels from the posterior cirri (5 and 6) and penis join to form the paired superior gastric vessels (Fig. 13). These vessels occupy a ventrolateral position on each side of the thoracic gut and decrease in caliber from their posterior origin. The superior gastric vessels give rise to a plexus covering almost the entire thoracic gut. Essentially the same pattern is shown in *P. polymerus* (Burnett, 1972). In one individual (of five *L. anatifera*) the efferent circulations from the left side of cirri 2 through 6 contributed to the superior gastric vessel (which in this case was divided into two vessels; Fig. 14). On the right side, the morphology was as described above.

The efferent cirral circulation also contributes to the peripheral circulation of the thoracic region (Fig. 15). In the dorsal part of the thorax the peripheral circulation is derived from the plexus of the thoracic gut circulation. The two peripheral circulations combine and their hemolymph flows anteriorly. At the cephalic-thoracic border, a vessel emanating from the thoracic peripheral circulation enters the cephalic filamentary appendage.

There is a peripheral connection between the thoracic and cephalic peripheral circulations, but as this area is remote from the site of injection, the Microfil rarely formed a continuous band from the thoracic to the cephalic peripheral-collecting circulations. The cephalic filamentary appendage (a type II filamentary appendage), however, serves as a less resistant connection between the two halves of the peripheral-collecting circulations. The cephalic transverse muscle, in contrast to that of *P. polymerus*, is surrounded by hemolymph from the cephalic peripheral circulation (Fig. 13).

The peripheral-collecting system of the prosoma has two regions. In the posterior part, the circulation is divided into a plexus that surrounds the testes (the testicular plexus). This is similar to the peripheral-collecting circulation of the thoracic region. In *L. fascicularis*, this plexus is more grossly constructed than in *L. anatifera* and in both a thin peripheral circulation arises from connections with the testicular plexus.

The testicular plexus and peripheral circulation connect anteriorly to the prosomal sinus (Figs. 13, 17), which is a half bowl-shaped sinus occupying the anterodorsal part of the body. This sinus is completely covered by a thin blanket of muscle (Fig. 18) that is sandwiched between the sinus and the cuticle of the prosoma.

As in *P. polymerus*, the prosomal sinus is connected by a pair of round openings (the prosomal valves, Fig. 17) to the rostral vessel. The morphology of the region appears to be as in *P. polymerus*, except the valve flaps of the rostral vessel do not appear to be present (this is probably due to vessel distortion so frequently observed in the injections of the lepadids).

The rostral sinus (Figs. 13, 17) also has a morphology similar to that of *P. polymerus*. This sinus receives blood from the oral cone, the adductor scutorum, and perhaps the prosomal sinus via the rostral vessel.

By shining a light through *L. fascicularis*, I observed that the cuticle between the adductor scutorum and the oral cone pulsates every 3-4 seconds at 22°C. Such movements probably result from the contraction of the rostral sinus muscles. However, for the rostral sinus to operate as a pump, a valve should be located between the rostral sinus and the anterior oral cone; none was found.

It appears that the rostral sinus pumps hemolymph through the rostral vessel and into the peduncle. The direction of flow is deduced from the position of the valves, partial injections of Microfil, and from my studies with *P. polymerus* (Burnett, 1972).

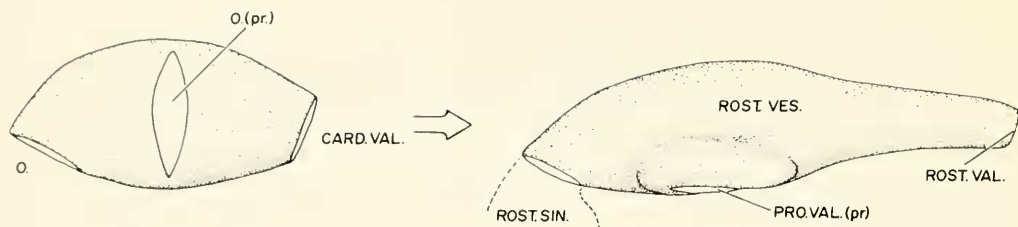


Figure 19. Comparison of the rostral vessel (right) with the heart of *Calanus finmarchicus* (left — redrawn from Lowe, 1935).

The structure of the vessel wall of the cephalic gut is like that of the midsagittal vessels in *P. polymerus*. Light microscopy shows an intima containing large branching fibers that become more diffuse a short distance from the intima. The spaces with no apparent circulation ventral to the gut are occupied by the seminal vesicles. These organs appear to have little circulation associated with them.

The distributive circulation of the four species differs in vessel number and caliber: the smaller species (*L. fascicularis* and *L. pectinata pacifica*) have fewer, larger caliber vessels than the larger species, suggesting that small barnacles have less complex circulation. *Conchoderma virgatum* and *L. fascicularis* are of similar size, but the former has more complex circulation.

The blood pump.—The location of the hemolymph pump in barnacles has been in dispute (Fyhn et al., 1973). From a study of serial sections of *Lithotrya valentiana*, Cannon (1947), placed it between the adductor scutorum and the base of the oral cone (the rostral sinus). He called this sinus the "blood pump" instead of a heart because the muscles are located within the sinus rather than encircling it. In *Balanus balanoides*, Gutmann (1960) argued that circulation takes place as a result of muscular activity or during cirral extension and retraction: during periods of inactivity contraction of muscles in the prosoma propel the blood. However, in inactive barnacles Blatchford (1970) observed movements in the region of the rostral sinus that he ascribed to circulatory movements.

I found by my observations on *L. fascicularis* that the rostral sinus probably acts as a blood pump for this species and for the other lepadid species.

DISCUSSION

Newman et al. (1969) postulated that the thoracican Cirripedia were derived from an ascothoracican-like maxillopodian ancestor and therefore are closely allied to the Copepoda. I noted (1972) the similarity of the heart of the copepod *Calanus finmarchicus* to the rostral vessel of *P. polymerus* (Fig. 19). The lepadid rostral vessel with its connection to the prosomal sinus has the same arrangement as in *P. polymerus*. The argument supporting the rostral vessel as being a vestigial heart is 1) the rostral vessel is essentially in a dorsal position and is properly oriented, 2) the openings into the rostral vessel correspond to the positions of the ostia in the copepod *Calanus finmarchicus* (Lowe, 1935), and 3) the rostral valve is homologous to the cardioarterial valve in the copepod heart.

Since the rostral vessel lacks musculature, I infer that during the evolution of the Cirripedia, heart function was shifted from the heart (rostral vessel) to the rostral sinus (an original part of the pericardial sinus). Why would there be a shift of heart function in the barnacles? In pedunculate barnacles contraction of the peduncle forces a large pulse of hemolymph into the body. Apparently, the only large sinus positioned to receive and store this extra hemolymph is the prosomal sinus. The prosomal sinus probably not only acts as the main venous sinus for the body, but also is involved in maintaining equilibrium between the peduncle and the body.

In the primitive thoracic cirriped, the heart was suspended in a sinus that was subject to increasingly high pressures as the peduncle became more dynamic. The net

effect of these increasingly high pressures would be collapse of the heart. A shift of blood pumping from the heart to a sinus where the muscles are intrinsically located would solve the problem of collapse.

The reason for splitting the primitive pericardial sinus into the prosomal and rostral sinuses is difficult to postulate. Perhaps this separation was present prior to the development of a peduncle and the consequent loss of heart musculature. Such a separation would be necessary if part of the pericardial sinus was to act as a reservoir and part as a pumping organ.

Regardless of the state of the peduncle, it must always receive oxygenated blood. This is accomplished by a continuous beating of the rostral sinus in which, no matter what the length of the peduncle, a constant volume of blood is pumped into the peduncle from the rostral sinus. Peduncular extension is probably mostly mediated by hemolymph from the prosomal sinus that was originally squeezed out of this sinus by contraction of the prosomal muscles.

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LITERATURE CITED

- Blatchford, J.G.
1970. Possible circulatory mechanism in an operculate barnacle. *Comp. Biochem. Physiol.*, 34:911-915.
- Burnett, B.R.
1972. Aspects of the circulatory system of *Pollicipes polymerus* J.B. Sowerby (Cirripedia: Thoracica). *J. Morph.*, 136:79-107.
- Cannon, H.G.
1947. On the anatomy of the pedunculate barnacle *Lithotrya*. *Philos. Trans. Roy. Soc. London., Proc. B* 233:89-136.
- Fyhn, H.J., J.A. Petersen, and K. Johansen
1973. Heart activity and high-pressure circulation in Cirripedia. *Science*, 180:513-515.
- Gutmann, W.F.
1960. Funktionelle Morphologie von *Balanus balanoides*. *Abh. senckenb. naturf. Ges.*, 500:561-603.
- Lowe, E.
1935. On the anatomy of a marine copepod *Calanus finmarchicus*. *Roy. Soc. Edinburgh, Trans.*, 58:561-603.
- Maynard, D.M.
1960. Circulation and heart function. *In*, Waterman, T.H. (ed.) *The Physiology of the Crustacea*. 1. Metabolism and Growth. Academic Press, New York. p. 161-226.
- Newman, W.A., V.A. Zullo, and T.H. Withers
1969. Cirripedia. *In*, Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology*. Part R. Arthropoda 4. Geological Society of America, Inc. Boulder Colorado, p. 206-295.

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APPENDIX ABBREVIATIONS

AD. SCUT.	adductor scutorum
AF. AD. SCUT.	afferent of the adductor scutorum
AF. CIR. VES.	afferent cirral vessel
AF. FIL. VES.	afferent filamentary vessel
AF. MAN. CIRC.	afferent mantle circulation
AF. MD.	afferent mandible circulation
AF. OR. C. VES.	afferent oral cone vessel
AN.	anus
ANT. OR. C. VES.	anterior oral cone vessel

CAR.	carina
CAR. VES.	carinal vessel
CARD. VAL.	cardioarterial valve
CEPH. FIL. AP.	cephalic filamentary appendage
CEPH. PER. CIRC.	cephalic peripheral circulation
CEPH. TR. M.	cephalic transverse muscle
CEPH. TR. M. CIRC.	cephalic transverse muscle circulation
CIR. 1	cirrus 1
CIRCUM. FL. M. CIRC.	circumflexor muscle circulation
CON. VES.	connective muscle
EF. CIR. VES.	efferent cirral vessel
EF. FIL. VES.	efferent filamentary vessel
EPI. SIN.	epineural sinus
EX. CUT.	exterior cuticle
FIL. AP.	filamentary appendage
G.	gut
GAST. GL.	gastric gland
GAST. PL.	gastric plexus
INF. GAS. VES.	inferior gastric vessel
IV. CIRC.	intervalve circulation
M.	mantle
MAX. GL. PL.	maxillary gland plexus
O.	ostium
O. (pr)	ostium (paired)
OR. C.	oral cone
OV. FR.	ovigerous frenum
P.	penis
PED.	peduncle
PED. VES.	peduncular vessel
PER. CIRC.	peripheral circulation
POST. INF. GAS. VES.	posterior inferior gastric vessel
POST. OR. C. VES.	posterior oral cone vessel
POST. SIN.	posterior sinus
PRO. M.	prosomal muscle
PRO. SIN.	prosomal sinus
PRO. VAL.	prosomal valve
PRO. VAL. (pr)	prosomal valve (paired)
ROST. M.	rostral muscle
ROST. SIN.	rostral sinus
ROST. VAL.	rostral valve
ROST. VES.	rostral vessel
SCUT. PL.	scutal plexus
SCUT. SIN.	scutal sinus
SCUT. VAL.	scutal valve
SCUT. VES.	scutal vessel
SUB. VES.	subintestinal vessel
SUP. GAS. VES.	superior gastric vessel
SUR. CIRC.	surface circulation
TER. PL.	tergal plexus
TEST. PL.	testicular plexus
THOR. FIL. AP.	thoracic filamentary appendage
THOR. PER. CIRC.	thoracic peripheral circulation
THOR. TR. M.	thoracic transverse muscle
VAL.	valve